Recruitment patterns of four tree species along elevation gradients in Mediterranean mountains: Not only climate matters

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ABSTRACT

Evidence of tree regeneration failure of some species in the Iberian Peninsula forests warns us about the impact that the global change may exert on the preservation of Mediterranean forests, such as we know them. Predictions agree about an exacerbation of the summer drought there, acknowledged as the main limiting factor for the recruits' survival. On the other hand, many studies have also proved the relevant role that local heterogeneity has over the spatial distribution of forest species recruitment by providing safe sites. Therefore, to unravel how climate interacts with local factors over juveniles' performance seems crucial for the design of successful management strategies that allow facing the global warming. Here, we surveyed the natural recruitment of four dominant tree species in seven mountainous regions in the Iberian Peninsula, along entire elevational ranges as surrogates of their climatic ranges. Two of them have alpine and temperate distributions with populations at their rear edge in the Spanish mountains: *Fagus sylvatica* and *Pinus uncinata*; and the other two have a genuine Mediterranean distribution: *Quercus ilex* and *Pinus nigra*. Our main goal was to analyze for each species the effect of climate, local factors (*i.e.* light availability, stand structure and ground cover) and the interactions among them to identify the main drivers leading the regeneration process, assessed in terms of presence, abundance and mean annual growth of juveniles. The results showed different environmental factors determining the recruitment patterns of each species. Nevertheless, they highlighted the pervasive role exerted by both climate and fine scale factors, particularly the co-occurring vegetation on recruits' abundance, and the light availability on their growth. Moreover, we found some interactions among annual mean temperature and local factors, suggesting that climate and local heterogeneity act hierarchically, *i.e.* the local conditions may mitigate or exacerbate the impact of climate on juveniles. These results advocate for further research to increase our knowledge on the complex net of interactions among factors involved in recruitment at different scales, which in turn should be taken into account and incorporated in forthcoming management strategies.

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1. Introduction

The Mediterranean Basin is one of the most vulnerable areas for biodiversity loss due to climate warming (Bakkenes et al., 2002; Thuiller et al., 2005). Predictions agree that increasing aridity and temperature, and more frequent extreme climatic events will occur there (Giorgi and Lionello, 2008; Nogués-Bravo et al., 2008). Therefore, since summer drought is acknowledged as the main limiting

factor for the performance of Mediterranean species, its exacerbation would be critical, especially for those species that have there their southernmost distribution limit (Castro et al., 2004; Hampe and Petit, 2005; Benavides et al., 2013).

Emergence and survival during the earliest life stages are critical for population dynamics (Harper, 1977). In fact, juveniles of woody species are considered to be more susceptible to climate and particularly to extreme events (Castro et al., 2005), responding quicker than adults to environmental changes (Lloret et al., 2009). Thus, viability and persistence of these populations rely heavily on the success of the current recruitment under the ongoing changing conditions. In Mediterranean areas, the coincidence of drought with high temperatures makes the summer season a critical bottleneck for life. Hence, recruitment in Mediterranean climate-type forests is episodic and depends on the appearance of favorable windows, *i.e.* rare wet summers entail the opportunity for establishment (Matías et al., 2012); whereas episodic events of severe drought occasionally cause massive seedlings' mortality (Herrero, 2012). In this line, recent studies carried out at large spatial scale using the data from the Spanish National Forest Inventory, revealed a relatively widespread regeneration failure in many forest stands, mainly in those dominated by pines like *Pinus sylvestris, P. uncinata, P. nigra*, species that naturally occur at the Iberian mountains (Vayreda et al., 2013; Carnicer et al., 2014; Tíscar and Linares, 2014). Additionally, other studies have shown a lack of regeneration of these and other species at their rear edge of their distributions (Peñuelas and Boada, 2003; Peñuelas et al., 2007; Benavides et al., 2013), sometimes accompanied by a gradual replacement with more heat-, drought- and shade-tolerant species, like *Quercus ilex*, that becomes a great competitor under the current climate and management changes (Galiano et al., 2010; Coll et al., 2013; Carnicer et al., 2014).

In parallel, encouraging studies have reported demographic responses that provide stabilizing processes (either by compensation or mitigation) and advocate resilience and stability in populations against the global warming (Doak and Morris, 2010; Lloret et al., 2012, 2013). For instance, Benavides et al. (2015) found higher growth rates at low elevations of different tree species along altitudinal gradients, despite a lower survival rate of recruits there. They suggested that these higher individual growths during seedling life stage bestow more chances to survive because they may overcome quicker this critical life stage, in terms of climate sensitivity and damage from browsers (Zamora et al., 2001), counterbalancing at population level the negative effect of global warming at the trailing edges. Moreover, they found a diminishing sensitivity to climatic conditions of the successive cohorts of juveniles (*i.e.* seedlings more sensitive than saplings), becoming relevant other fine scale factors that attenuate the effects of climate on saplings
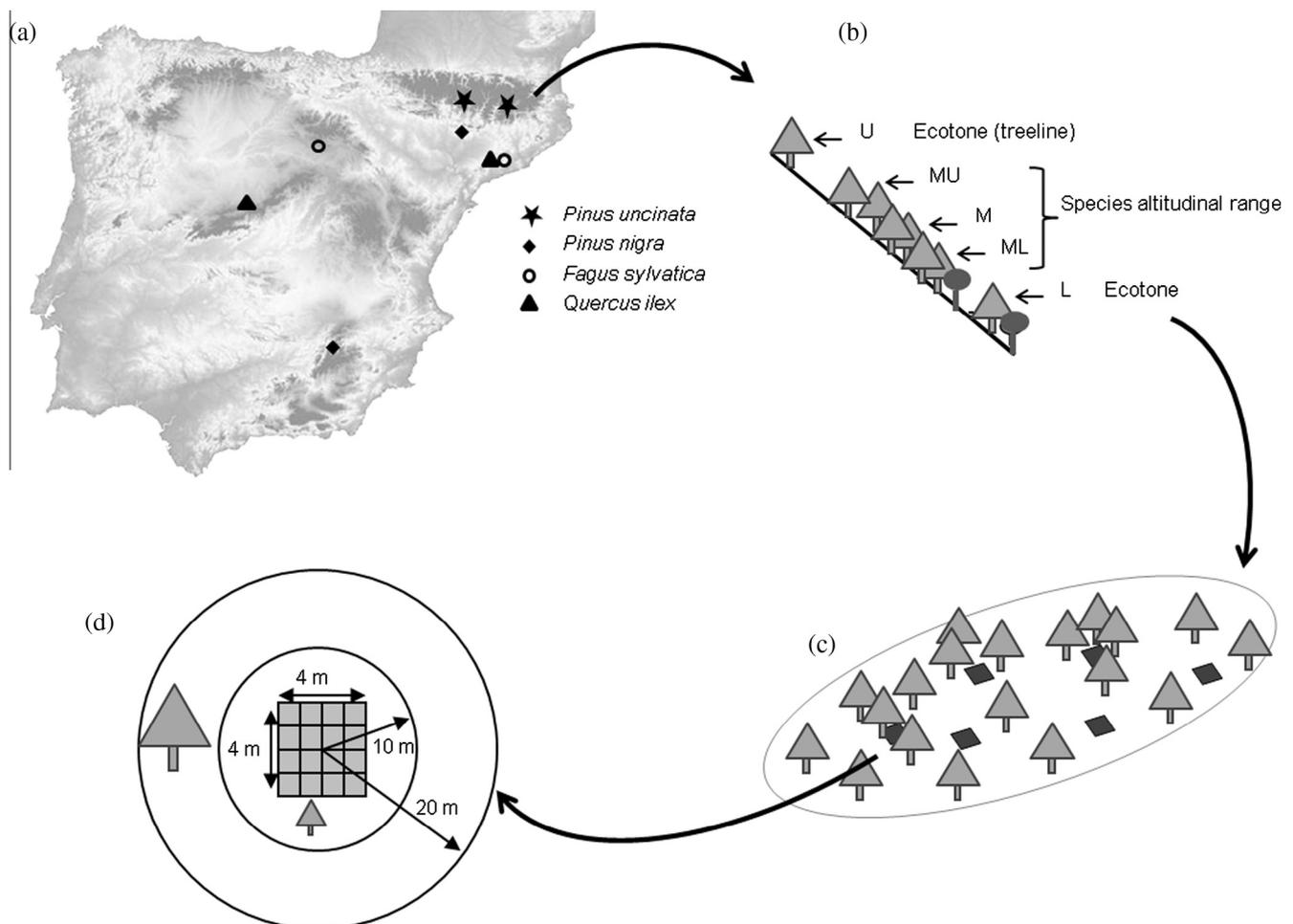
Fig. 1. Sampling design: (a) site locations, (b) diagram of transects layout within a site, (c) display of plots layout (gray squares) within a transect, and (d) plot design. Two sites for every species were sampled. Within each location, five transects were established at five elevations (three in sites with *Quercus ilex*) coded as: upper (U), mid-up (MU), middle (M), mid-low (ML) and lower (L) transects. Within each transect, six plots were established, three of them under closed canopy and the other three in gaps. Each plot encompasses a 4 × 4 m central squared regeneration plot – with 16 subplots of 1 m² size, and round plots where adult trees were mapped and measured: a 10-m radius area for every adult tree (>7.5 cm dbh), and 20-m radius circle for bigger trees (>20 cm dbh).

Table 1
Description of the study sites, with ranges or mean values (with the standard deviation in brackets) of main environmental characteristics (T: mean annual temperature, P: annual mean precipitation, BA: the basal area in 10 m-radius plots, Density assessed considering the conspecific adult individuals). Climatic variables were obtained at plot level using the Digital Climatic Atlas of the Iberian Peninsula, (Ninyerola et al., 2005).

Site	Target species	Coordinates	Altitudinal range (m)	T range (°C)	T mean (°C)	P range (mm)	P mean (mm)	Slope (%)	Density (trees ha^{-1})	BA (m^2 ha^{-1})	Dominant tree species downslope	Dominant tree species upslope
Montseny	Q. ilex	41°45′N 2°29′E	716–1092	9.8–12.3	11.2 (0.8)	811.2–1147.2	955 (112)	58 (7)	522.0 (383.2)	40.7 (14.1)	–	F. sylvatica
Guadarrama	Q. ilex	40°52′N 4°02′W	1138–1360	9.9–10.9	10.4 (0.4)	762.7–810	787 (16)	12 (11)	359.0 (203.3)	19.2 (13.5)	–	P. sylvestris
Solsona	P. nigra	42°10′N 1°42′E	567–1317	8.7–12.2	10.4 (1.2)	730.3–985.7	812 (65)	56 (13)	756.5 (314.2)	27.3 (13.3)	Q. faginea, Q. ilex	Treeline
Segura	P. nigra	38°28′N 2°27′W	1122–1498	11.3–12.6	12.0 (0.5)	698.3–980.2	843 (83)	33 (11)	235.5 (145.4)	26.3 (12.6)	P. pinaster	Treeline
Aigüestortes	P. uncinata	42°36′N 1°04′E	1817–2405	2.9–6.2	4.6 (1.0)	701.8–988.6	839 (112)	55 (14)	403.2 (308.5)	29.0 (20.5)	Abies alba	Treeline
Cerdanya	P. uncinata	42°21′N 1°27′E	1730–2198	3.9–6.3	5.2 (0.8)	1006–1209.5	1069 (68)	48 (18)	484.9 (333.8)	31.7 (14.5)	Abies alba	Treeline
Montseny	F. sylvatica	41°46′N 2°28′E	913–1614	6.9–11.8	9.0 (1.7)	811.2–1274.5	1066 (141)	52 (11)	522.0 (383.2)	40.7 (14.1)	Q. ilex	Treeline
Cebollera	F. sylvatica	42°04′N 2°36′W	1173–1798	6.1–9.3	7.8 (1.1)	692.5–898.1	774 (48)	35 (11)	569.8 (455.3)	30.6 (12.9)	Q. pyrenaica, Ilex aquilinum	Treeline

performance. Within this context, other studies in Mediterranean areas highlighted the decisive role exerted by these local environmental conditions (biotic and abiotic factors) over the juveniles' survival and growth, leading to aggregated patterns in safe sites (Quero et al., 2011; Ameztegui and Coll, 2015). In particular, the nurse role of shrubs, ameliorating harsh conditions imposed by summer drought or herbivore damages, is quite acknowledged in these areas (e.g. Gómez-Aparicio et al., 2004; Quero et al., 2011).

Understanding how climate interacts with local factors over juveniles' performance in order to mitigate global warming and propose management strategies to face it, is a research priority that, so far, got little attention and effort. Moreover, it is especially interesting to compare the performance of species at their rear edge (more vulnerable facing climatic changes) with others at the center of their ranges to identify global responses to current warming, to predict future species distributions and community compositions in Mediterranean areas, and to design strategies to mitigate the impact of climate change over standing forests. In the present study, we contribute to this goal analyzing the main factors that influence the regeneration of four of the main dominant tree species in the Iberian Peninsula forests. Two of them have alpine and temperate distributions with populations at their rear edge in the Spanish mountain ranges: Mountain pine (Pinus uncinata Ram.) and European beech (Fagus sylvatica L.); and the other two species have a typical Mediterranean distribution: Holm oak (Quercus ilex L.), with an ample presence in the Iberian Peninsula, and European black pine (P. nigra Arn. ssp. salzmannii (Dunal) Franco), a Mediterranean mountainous pine. In particular, we studied the effect of climate, local factors and the interactions among them to identify the main drivers leading the regeneration process, assessed in terms of presence (occurrence), abundance and mean annual growth of juveniles. We surveyed their entire elevational range in mountainous areas as surrogates of the climatic range that each species experiences along its latitudinal distribution. Using elevation as a surrogate for climate range is a useful tool to study responses under different climatic scenarios, minimizing differences due to genetic variability and other potential confounding variables determined by the specific characteristics of a region (Körner, 2007).

2. Material and methods

2.1. Study sites

Data gathering was conducted in seven mountainous areas across Spain in late spring and summer in 2010 and 2011 (Fig. 1). The entire sampling required two years, but each site was sampled only once. For every species we sampled two pure natural forest sites located in different mountain ranges, along five elevational transects. The stands had neither visible signs of plantations, nor any evidence of management that could affect the current recruitment. The upper and the lower transects were placed in the ecotones of each target species with the adjacent communities. In the majority of the cases, the upper transects were located at the treeline of these mountain ranges (i.e. transition from the uppermost closed forests to the treeless mountainous vegetation). The three intermediate levels were located within the altitudinal range of each species, with at least 100 m difference in altitude among them. Those at the ends were located near the boundary with the ecotones, and the intermediate one in the middle of the range. For Q. ilex's sampling, we only considered the three superior levels (transects) as this species has no low elevation limit in the Iberian mountains. Table 1 shows the main characteristics of the study sites.

2.2. Recruitment sampling and measurements of environmental variables

We established six plots within each elevational transect, separated at least 100 m. Three plots were randomly located under closed canopy, and the other three in more open areas to include contrasting light conditions within each forest and elevation, avoiding ravines, boulders or other geomorphologic elements which could bias our measurements ameliorating the effect of climate by local physiography (Dobrowski, 2011). In the center of every plot we recorded the number of juveniles in a 4×4 m plot (16 m^2-sized), recording the number per square meter, i.e. each plot encompassed 16 observations of juveniles' density from its 16 subplots of 1 m^2 size. We counted the seedlings with at least one year, i.e. survivors after the first summer drought, considered the main bottleneck for recruitment in Mediterranean areas (Jordano and Herrera, 1995; Castro et al., 2004; Linares and Tíscar, 2010), up to juveniles 1.50 m tall. Juveniles of resprouting species (Q. ilex and F. sylvatica) were correctly identified from vegetative offsprings (not considered in this study), following Espelta et al. (1995). We estimated their age by counting the terminal bud scars (internodes) along the main stem and we sorted them into two different age classes (Espelta et al., 1995), assuming a different sensitivity to the environment (Collins and Carson, 2004; Benavides et al., 2015): S1: seedlings – from one to five years; S2: saplings – over five years; (hereafter juvenile is only used when age is not relevant and both age classes are considered). We identified the current shoot (not considered for the study as the growing season was not over) and we measured the primary shoot growth of the main stem not damaged by herbivores in previous years (growths occurred in 2007, 2008 and 2009), and averaged them. Shoot growth is a good indicator of environmental favorability (Willms et al., 1998), as well as the impact of drought conditions on plant growth (Mutke et al., 2003). Hence, we used mean annual growth as a proxy of their individual performance.

To evaluate the effects of climate, we rendered elevation and latitude data of each plot into climatic variables using the Digital Climatic Atlas of the Iberian Peninsula (Ninyerola et al., 2005), specifically we obtained the annual mean temperature (°C) and mean annual precipitation (mm).

The local environmental variables were selected assuming their influence on the recruitment, either by modifying the physical environment or by competing for resources (in the case of co-occurring vegetation). At plot level, we measured the slope that may hamper the establishment, and the light availability, crucial for plant development. Light was assessed as the global site factor (GSF), defined as the proportion of global solar radiation at a given location relative to that in the open. To assess it, we took one hemispherical photograph in the center of each plot at 50 cm above the ground and we analyzed the images using the software HemiView 2.1 (Delta-T Devices, UK). In terms of biotic conditions at plot level, all adult trees (diameter at breast height, dbh, over 7.5 cm) within a 10 m radius around the regeneration frame were mapped and we measured their dbh, and then calculated the basal area (expressed as m^2/ha) per plot as an index of competition with adult trees. This radius size was consistent with that used in other tree competition studies (He and Duncan, 2000; Gómez-Aparicio et al., 2011).

Finally, at microhabitat scale, we visually estimated in every 1-m^2 subplot the cover in percentage of rocks that may physically impede juveniles' thriving, and the cover of shrubs and herbs, that may facilitate or compete with them. Moreover, a potential fecundity index was assessed for each subplot, considering the conspecific adult trees previously mapped within the 10 m radius, together with those bigger than 20 cm of dbh located between 10 and 20 m from the center of the plot. This unitless index has two components (see Ribbens et al., 1994): one related to the amount of seeds

that an adult tree can produce (seed rain), proportional to the tree size (dbh); and another that accounts for the seed dispersal capacity and assumes an exponentially decline as the distance between a particular tree and the center of each subplot increases (Ribbens et al., 1994; Gómez-Aparicio et al., 2011).

$$FI_i = \sum_{j=1}^{n} dbh_j^2 \cdot e^{-dist_{ij}}$$

where FI_i is the fecundity index for subplot i within a plot with n trees ($j = 1, 2, \ldots n$), and $dist_{ij}$ is the distance of tree j to the center of subplot i.

2.3. Statistical analyses

The density of individuals of both age classes (seedlings and saplings) along the elevation for every species was compared using the Mann–Whitney U test. Similarly, the mean annual growth of each species were compared along the five different transects (elevational levels) using one-way ANOVA after a log-transformation.

Next, we evaluated the effects of climate (mean annual temperature and precipitation) and local factors on the density and mean annual growth of juveniles of each species. Previous to the modelling process, we carried out an analysis of correlation among the local variables to detect multicollinearity among them (Zuur et al., 2010), (see Supplementary Information Table A.1). When two variables were highly correlated ($\rho > 0.4$) for at least two species, we removed from the pool the variable with less direct implications on recruitment. In particular, we discarded basal area and slope because they were highly correlated to GSF, and to rock cover and climatic variables, respectively. Basal area was considered an index for competition with adult trees, and since competition among adults and juveniles is expected to be mainly related to light availability, we kept GSF. Both rocks and slope impair physically the establishment of recruits, however rockiness data were taken at subplot level and slope for the whole plot being less accurate and precise than the former. In summary, we kept as explanatory variables, together with temperature and precipitation, the cover of herbs, shrubs, rocks, GSF and FI (the latter only considered for density data models, as it is not relevant for growth). In the case of F. sylvatica, we had scarce observations and we decided to simplify more the models. Hence, we discarded also the cover of herbs and shrubs because of their overall lack in most of the plots and their high correlation with light availability (GSF). The interactions of annual temperature with GSF, annual precipitation, and the cover of understorey vegetation were included in the model, as well as the quadratic term of temperature to consider non-monotonic responses along the gradient. Non-linear responses to other variables were not considered to avoid a great complexity of the models.

Different statistical methods have been previously used to model regeneration and figure out the environmental factors that mainly drive this process (a review in Moreno-Fernández et al. (2015)). In the present study, the density data of juveniles per m^2 (data at subplot level) of each species followed a Zero-Inflated Poisson distribution (ZIP), as no recruit was found in a large amount of the subplots surveyed, specifically in 72.2%, 80.4%, 93.9% and 76.1% of the subplots for P. uncinata, P. nigra, F. sylvatica and Q. ilex respectively. Models fitting ZIP distributions (ZIP models) account for this excess of zeros avoiding the underestimation of the number of zeros and the overestimation of large count occurrence (Hall, 2000; Affleck, 2006; Fortin and De Blois, 2007; Benavides et al., 2013). They consist of a two-step analysis, a binomial distribution model analyzing the occurrence (observing or not recruits), and a Poisson distribution model, conditional on the first, analyzing the abundance (number of recruits), both

processes evaluated all at once. Here, we decided to neglect the age class and pool seedlings and saplings to increase the sample size due to the low number of observations in some plots and the number of parameters to estimate (the environmental variables affecting both the occurrence and abundance independently). On the other hand, the data of mean annual growth of juveniles followed a normal distribution after a log-transformation, and due to the larger sample size of this response variable (data at individual level) we run the analyses for each age class separately.

We added random components into the intercepts of the linear predictors of the models (Hall, 2000) due to the hierarchical structure of our data, with likely different level of correlation among observations within the same subplot (for growth data), plot, transect or site. We considered 'site' as a fixed effect, as this variable only had two levels, therefore not enough to estimate among-site variance (Bolker et al., 2009). The rest of the nested design (subplots within a plot, plots within a transect) was considered in the random component for analysis of mean annual growth. However, the statistical procedure used for ZIP modelling recommends the use of just one random effect due to the complexity of the likelihood function (that includes both processes: the binomial and Poisson models) and problems detected with the convergence of the model. Thus, we preliminary fit the saturated models including both effects separately, transect and plot, and we chose the model which harbored more variability (*i.e.* plot) using the Akaike's Information Criterion (AIC). Concerning the explanatory variables (fixed effects), we selected the best model following the principle of parsimony to find the simplest model that was not significantly worse than any more complicated in terms of AIC. We assumed that a model was better than the previous one when the improvement of AIC was higher than two units, *i.e.* at least two units smaller (Burnham and Anderson, 2002). We started by running the

saturated model, and then we removed one non-significant variable each time (Zuur et al., 2009).

The Zero-Inflated Poisson Mixed Models (ZIP models) for density data and the Generalized Linear Mixed Models (GLMM) for growth data were both fit for each species separately using the SAS procedure NLMIXED (Pinheiro and Bates, 1995; SAS Institute Inc. 2008. SAS/STAT 9.2) that allows the optimization of the customized likelihood function of the ZIP models.

3. Results

3.1. Abundance and growth data across the altitudinal levels

The total amount of juveniles recorded and used in the occurrence and abundance analyses were 1541 juveniles, sorted into 259 of *Q. ilex*, 564 of *P. nigra*, 608 of *P. uncinata* and 110 of *F. sylvatica*. The altitudinal distribution of juveniles (Fig. 2a) showed that seedlings (S1) of both Mediterranean species, *Q. ilex* and *P. nigra*, appeared mainly at higher altitudes compared to the saplings (S2), whose distributions were more regularly spread along the entire altitudinal range. For the other two species, there was no significant difference between age classes, with a distribution slightly skewed toward higher altitudes in the case of *P. uncinata*, while individuals of *F. sylvatica* appeared mainly in the lower areas of its range.

For growth analyses, and after excluding the individuals damaged, we counted 1394 juveniles, sorted into 233, 487, 584 and 90 juveniles of *Q. ilex*, *P. nigra*, *P. uncinata* and *F. sylvatica*, respectively. The annual mean growth averaged per species and transect showed a different pattern between the age classes (Fig. 2b). Seedlings showed a generalized lower growth at higher elevations (but
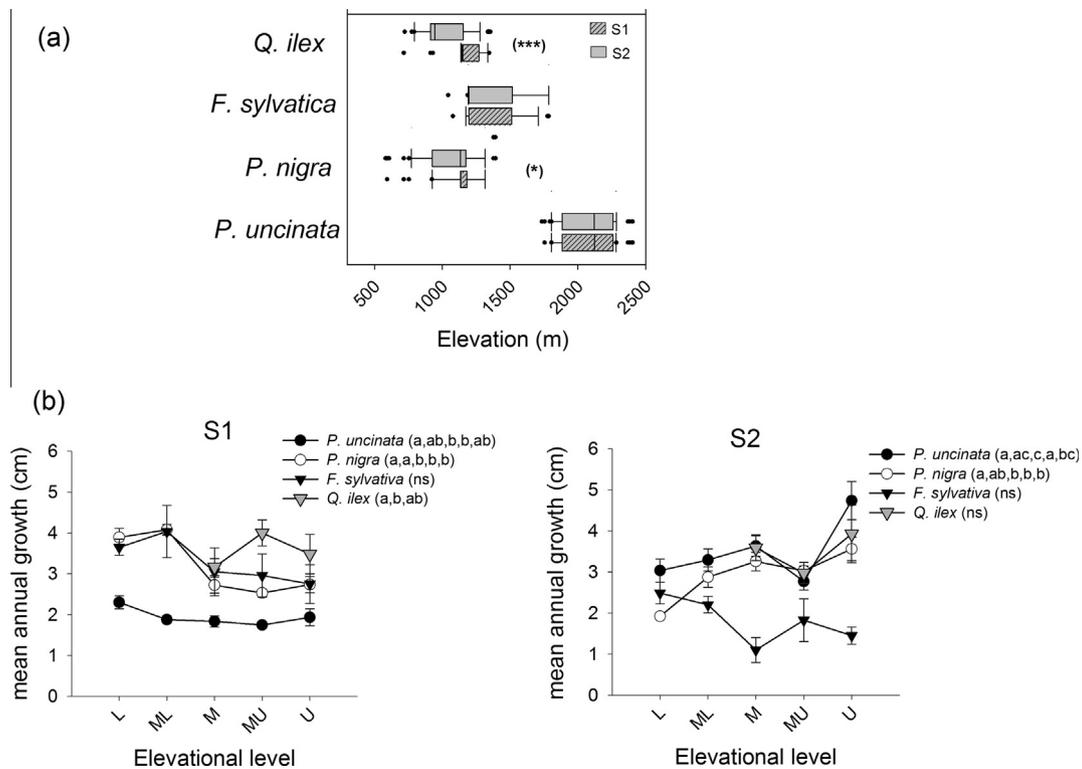
Fig. 2. a) Distribution of juveniles along the elevation for both age classes (S1: seedling – from 1 to 5 years, S2: saplings – over 5 years) of every species (according to Mann–Whitney *U* test * *p* < 0.05; *** *p* < 0.001). (b) Mean growth averaged per elevational level and species for both age classes S1 and S2. (L: lower transect; ML: mid-low transect; M: middle transect; MU: mid-up transect; U: upper transect). Different letters show significant difference among the elevational levels according to Kruskal–Wallis test and one-way ANOVA.

Table 2
Final Zero-Inflated Poisson Mixed Models for the occurrence (absence) and abundance of juveniles. (Dashes mean variables not included in the final model; T: annual mean temperature, °C; P: annual precipitation, mm; GSF: global site factor; Herbs, Shrubs and Rocks expressed as % of cover; ΔAIC: difference in AIC referred to the saturated model; EF: efficiency of modelling[a]; n = sample size, number of subplots surveyed; SE: standard error; NC: not considered in the saturated model; * p < 0.05; ** p < 0.01; *** p < 0.001). The parameters estimated in the binary part (occurrence) are referred to the probability P finding no recruit (absence), being 1 – P the probability of presence.

		Pinus uncinata ΔAIC = 24.1 EF = 0.456; n = 960 Estimate (SE)	Pinus nigra ΔAIC = 23.6 EF = 0.475; n = 960 Estimate (SE)	Fagus sylvatica ΔAIC = 26.6 EF = 0.416; n = 960 Estimate (SE)	Quercus ilex ΔAIC = 18.8 EF = 0.358; n = 480 Estimate (SE)
Occurrence	Intercept	−13.684 (4.254)**	0.302 (0.417)	−1.521 (1.176)	−3.229 (0.849)
	Site	–	−5.935 (1.090)***	–	–
	P	0.0168 (0.004)***	–	–	–
	Shrubs	−0.107 (0.048)*	–	NC	–
	Rocks	0.046 (0.014)**	–	–	–
	GSF	−9.406 (2.999)**	–	–	–
	Shrubs × T	0.029 (0.011)*	0.005 (0.001)***	NC	–
Abundance	Intercept	−7.567 (2.694)**	−14.119 (2.618)***	23.613 (8.600)*	−6.286 (4.388)
	Site	–	–	–	1.152 (0.534)*
	T	3.658 (1.178)**	0.328 (0.207)	−10.3483 (2.081)***	1.3126 (0.313)***
	T²	−0.382 (0.125)**	–	0.687 (0.132)***	–
	P	–	0.011 (0.002)***	0.0166 (0.003)***	−0.011 (0.003)***
	Herbs	−0.010 (0.002)***	0.081 (0.020)***	NC	−0.011 (0.006)*
	Shrubs	−0.044 (0.015)**	–	NC	–
	Herbs × T	–	−0.008 (0.002)***	NC	–
	Shrubs × T	0.008 (0.004)*	–	NC	–

[a] The modelling efficiency (EF) is assessed through: $EF = 1 - \left[\frac{\sum_{ij}(y_{ij} - \hat{y}_{ij})^2}{\sum_{ij}(y_{ij} - \bar{y}_{ij})^2}\right]$ where y_{ij} and $\hat{y}_{ij}$ are the observed and predicted data, and $\bar{y}_{ij}$ is the mean value for the response variable.

for Q. ilex), while the opposite trend was found in saplings, except for F. sylvatica, although with non-significant variation along elevation.

3.2. Factors affecting occurrence, abundance and growth patterns of regeneration

The variables considered in this study, both climatic and local, barely explained the occurrence of recruits, but for P. uncinata; while abundance and growth of juveniles were affected by the variables considered, to a greater or lesser extent (Tables 2 and 3).

The ZIP models showed that the abundance of juveniles of every species was significantly influenced by the climatic variables (temperature and/or precipitation). The selected models for the two species with a northerner distribution, F. sylvatica and P. uncinata, showed a clear quadratic effect of mean annual temperature (hollow-shaped curve for F. sylvatica and hump-shaped for the P. uncinata); while the model for Q. ilex showed a positive linear effect of temperature on juveniles' abundance. Precipitation favored the density of juveniles of F. sylvatica and P. nigra, but affected negatively the abundance of Q. ilex and the occurrence of P. uncinata recruits (Table 2).

The models also showed the direct influence of some local factors related to the co-occurring vegetation on the recruitment pattern (Table 2). We found a negative effect of the cover of herbaceous plants on the abundance of Q. ilex and P. uncinata. In addition, we detected indirect effects of these biotic variables, interacting with temperature, like the effect of the shrub layer on density of P. uncinata and occurrence of P. nigra juveniles, and the effect of herbs on the abundance of the latter (Fig. 3). These interactions showed that moderate cover of shrubs (<50%) facilitated the presence of juveniles of both pine species under not very stressful temperatures; and that the cover of herbs impaired the abundance of P. nigra juveniles, especially at high temperatures (more heat stress).

The GLMMs showed that GSF was the variable that affected the mean annual growth of juveniles in most of the cases, together with climatic variables (Table 3). However, the relationships were

age- and species-specific. Juveniles of P. uncinata were affected by the interaction of temperature and GSF, with a better performance in gaps with higher temperature, or in cooler places under canopy (Fig. 4). S2 were also favored by annual precipitation and the lack of rocks (Table 3). Growth of P. nigra seedlings (S1) were positively affected by temperature and GSF. Light favored also the annual mean growth of Q. ilex saplings (S2); while S1 were affected by temperature interacting with annual precipitation (Fig. 4). This interaction showed that the growth increased at higher temperatures when the precipitation was also high, and with low both precipitation and temperature. Finally, the models obtained for F. sylvatica did not capture any variable affecting growth, but the rockiness hampering the growth of S1, although the sample size of this species was much lower compared to the other species.

4. Discussion

The results of the present study showed the key role exerted by both climate and fine scale factors on the distribution and performance of four tree species recruitment along altitudinal ranges, being the direction and relevance of these effects species-specific according to the idiosyncrasy of each species. They also highlighted that the use of complete altitudinal gradients gives valuable information about how a species thrives along complete climate gradients, and why it can be considered a very efficient alternative to experimental settings as surrogates of performance of tree species along the global distribution range (Körner, 2007). Besides, they pointed at the use of coexisting genuine Mediterranean species together with species at their rear edge to infer hints on recruitment strategies and future composition of forest communities.

4.1. Relationship between climate and juvenile patterns along altitudinal gradients

The two Mediterranean species, Q. ilex and P. nigra presented an asymmetrical distribution, with the young cohort (seedlings) being more abundant at higher elevations than the old one (saplings). This suggests better conditions to survive the first years at higher

Table 3
Final Generalized Linear Mixed Models for the mean annual growth of juveniles. (Dashes mean variables not included in the final model; T: annual mean temperature, °C; P: annual precipitation, mm; GSF: global site factor; Shrubs and Rocks expressed as % of cover; ΔAIC: difference in AIC referred to the saturated model; EF: efficiency of modelling[a]; *n*: sample size, number of juveniles recorded per species and age class; SE: standard error; S1: seedlings from 1 to 5 years; S2: saplings over 5 years; NC: not considered in the saturated model; * *p* < 0.05; ** *p* < 0.01; *** *p* < 0.001).

		P. uncinata ΔAIC = 63.4 EF = 0.298; *n* = 252 Estimate (SE)	*P. nigra* ΔAIC = 53.4 EF = 0.484; *n* = 195 Estimate (SE)	*F. sylvatica* ΔAIC = 10.9 EF = 0.192; *n* = 64 Estimate (SE)	*Q. ilex* ΔAIC = 9.8 EF = 0.277; *n* = 109 Estimate (SE)
S1	Intercept	9.027 (2.896)**	−2.586 (0.992)*	3.992 (0.295)***	371.00 (111.36)**
	T	−2.819 (1.078)*	0.463 (0.077)***	–	−32.109 (9.309)**
	T²	0.257 (0.1)*	–	–	–
	P	–	–	–	−0.451 (0.141)**
	Rocks	–	–	−0.020 (0.009)*	–
	GSF	−5.858 (2.2230)*	3.617 (1.304)*	–	1.133(0.743)
	GSF × T	1.436 (0.477)**	–	–	–
	T × P	–	–	–	0.039 (0.012)**
		ΔAIC = 28.7 EF = 0.294; *n* = 332 Estimate (SE)	ΔAIC = 44.11 EF = 0.514; *n* = 292 Estimate (SE)	ΔAIC = 15.2 EF = 0.357; *n* = 26 Estimate (SE)	ΔAIC = 31.7 EF = 0.358, *n* = 124 Estimate (SE)
S2	Intercept	0.073 (1.059)	1.845 (0.824)*	1.814 (0.258)***	3.175(0.557)***
	Site	–	2.131 (0.613)**	–	−1.185(0.533)*
	T	−0.764 (0.170)***	–	–	–
	P	0.007 (0.001)***	–	–	–
	Shrubs	–	0.014 (0.006)*	NC	–
	Rocks	−0.028 (0.010)**	–	–	–
	GSF	–	2.729 (3.155)	–	2.917 (1.072)*
	GSF × T	0.765 (0.201)***	–	–	–

[a] The modelling efficiency (EF) is assessed through: $EF = 1 - \left[\frac{\sum_{ij}(y_{ij} - \hat{y}_{ij})^2}{\sum_{ij}(y_{ij} - \bar{y}_{ij})^2} \right]$ where y_{ij} and $\hat{y}_{ij}$ are the observed and predicted data, and $\bar{y}_{ij}$ is the mean value for the response variable.

elevations, likely in terms of precipitation. Recent studies carried out in the Iberian Peninsula showed an upward shift of *Q. ilex* recruits toward cooler areas (Urbieta et al., 2011; Vayreda et al., 2013; Carnicer et al., 2014), as seedlings appeared negatively affected by low soil moisture and increased temperature (Caldeira et al., 2014). Accordingly, its growth model in this study showed that seedlings grew less in places more prone to droughts (warmer and drier). The models for *P. nigra* showed that temperature boosted seedling growth, but it was annual precipitation the climatic variable that significantly favored the abundance of juveniles. This last result concurs with other studies pointing out that water supply, especially in early summer, is the main limiting factor for the regeneration of this species (Urbieta et al., 2011; Vayreda et al., 2013; Tiscar and Linares, 2011).

Nevertheless, the ZIP model for *Q. ilex* showed a positive effect exerted by temperature and negative by precipitation over the abundance of juveniles, which runs in the opposite direction. The divergences with the former studies may be related to the impossibility for analyzing both cohorts separately, and most likely, due to the elevational range surveyed in this study that did not cover the whole climatic gradient of this species in the Iberian Peninsula. Here, we just considered the three upper transects (over 700 m a.s. l.) because there was no low limit for this species.

The response of the other species to climate, the non-genuine Mediterranean, did not exhibit a common pattern. Juveniles of *P. uncinata,* in agreement with some previous studies, were negatively affected by the annual temperature, growing more at higher elevations (Grau et al., 2013; but see Ameztegui and Coll, 2013), and presented a hump-shaped relationship with the abundance of juveniles (Coll et al., 2013). This non-linear relationship implies the existence of an optimum where juveniles peaked, that occurred at slightly higher altitudes than the mean altitudinal range of the stands, and decreased very rapidly as altitude approached the treeline. Similar asymmetric presence of elevational optima of juveniles upwards, compared to the adults' mean distribution, have already been detected not only for this species (Batllori and

Gutierrez, 2008), but also for others (Gworek et al., 2007; Lenoir et al., 2009; Benavides et al., 2013; but see Rabasa et al., 2013). These studies suggest the existence of an ongoing upward shift driven by warming, that may act either directly on the recruitment of the study species or indirectly by limiting its competitive ability compared to other species more heat- and drought-tolerant (Lenoir et al., 2010; Ameztegui and Coll, 2013). Moreover, annual precipitation appeared as an important factor, although it exerted a differential effect over the occurrence of juveniles (negative) and their performance (positive over the growth). This contradictory result might be related to indirect effects of local factors that impair the recruitment, but once seedlings are recruited, they performed better with high precipitation. However, we acknowledge that this claim should be taken with caution because extrapolations of climatic variables, like precipitation, harbor great uncertainty at these high elevations due to the scarce meteorological stations up there (Benavides et al., 2007).

The outcomes for *F. sylvatica* showed the overall lack of recruitment with a small amount of juveniles. Likewise, Vayreda et al. (2013) who analyzed the data from the Spanish National Forest Inventory, found low abundance or no saplings in around 70% of the total plots where this species dominates in the canopy. These results reflected the difficulties that this species might be experiencing in these southern marginal areas of its distribution, where summer drought greatly constraints *Fagus* recruitment (Kunstler et al., 2007; Silva et al., 2012). In this direction, we found that precipitation favored the abundance of juveniles, as earlier studies carried out in other European countries did (Kunstler et al., 2007; Klopcic et al., 2012; Silva et al., 2012). Nevertheless, we found a hollow-shaped relationship of juvenile abundance with the annual temperature, caused by a surprisingly high density of them at low elevations. This unexpected result in the trailing area of the species distribution disagreed with previous studies conducted in northeastern Spain, which evidenced an upslope shift of this species during the last century (Jump et al., 2007; Peñuelas et al., 2007). We infer that other factors, different from climate, underlie this trend
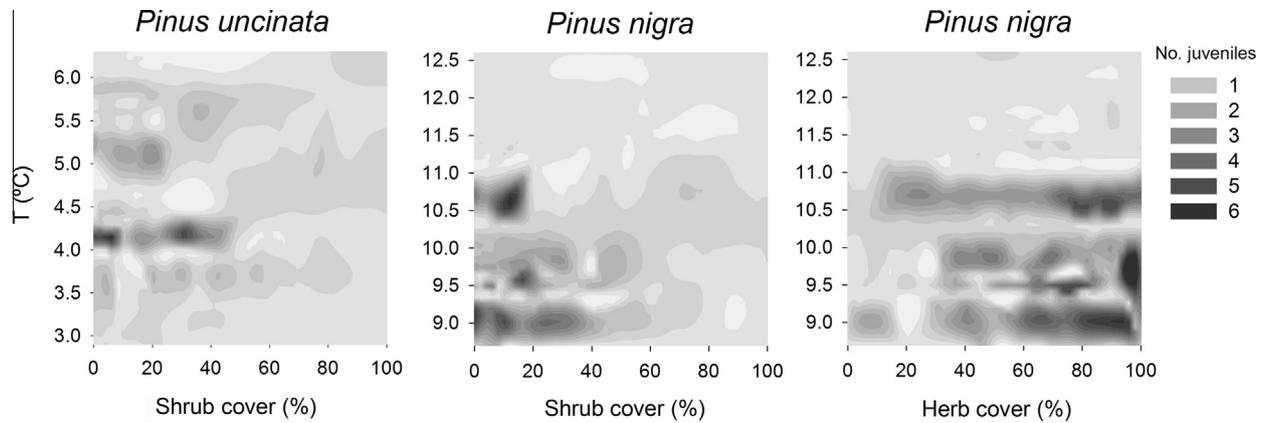
Fig. 3. Effect of the significant interactions among mean annual temperature (T, °C) and different biotic variables on the density of juveniles estimated using Zero-Inflated Poisson (ZIP) mixed models. The predicted values of density is the result of multiplying the predictions for both ZIP submodels, the occurrence submodel (binomial model) that gives the probability of finding a recruit $(1 - P)$, and the abundance submodel (Poisson model) that returns the number of predicted juveniles when they are presence (λ).
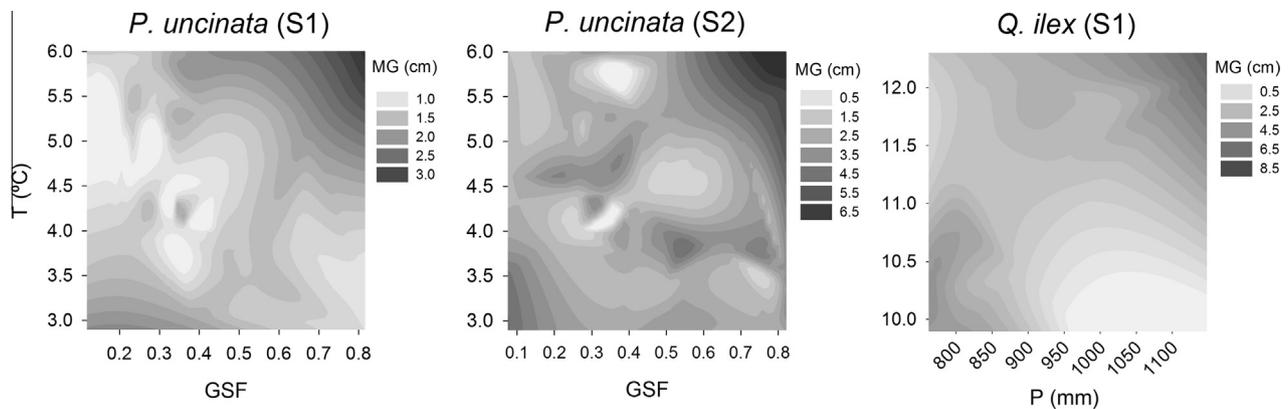
Fig. 4. Effect of the significant interactions among mean annual temperature and other variables on the annual mean growth (MG, cm) of juveniles estimated using Generalized Linear Mixed Models. (T: mean annual temperature, °C; GSF: global site factor; P: mean annual precipitation, mm; S1: seedling from 1 to 5 years; S2: saplings over 5 years).

and conceal the species primary response to climate in our study sites. Indeed, the lower transects of these sites had different stand structure, probably due to a different former management, with lower densities of multi-stemmed individuals than at mid-upper elevations (see Supplementary Information Fig. A2).

4.2. Downscaling: the importance of local factors and its interaction with climate

Recruitment is strongly conditioned by the spatial local heterogeneity as well. The structure and composition of the stand (adult trees) determines the quantity of seed rain, and together with the understorey vegetation and micro-topographic conditions, they determine the regeneration niche (Grubb, 1977), *i.e.* the fine-scaled environment that allows juveniles to thrive.

In our study, considering the variables related to the stand structure, *i.e.* GSF (light availability) and the fecundity index (proxy for the potential seed rain), we found that the light availability favored the presence of *P. uncinata* juveniles, in accordance with its shade-intolerance nature (Batllori et al., 2009). However, its main effect was exerted over the growth of juveniles, as earlier studies reported in Mediterranean mountains (Gómez-Aparicio, 2008; Matías et al., 2011; Ameztegui and Coll, 2011, 2013; Barbeito et al., 2012; Benavides et al., 2013; Grau et al., 2013; Caldeira et al., 2014). In particular, the growth of *P. nigra* seedlings and *Q. ilex* saplings were both boosted by light; and its positive effect over the juveniles of *P. uncinata* was exacerbated by

temperature, appearing higher growths in the gaps (high light availability) of warmer places (lower elevations). On the other hand, we found no effect of the fecundity index on the density of juveniles of any study species. This suggests that, since our forest stands were monospecific, the seed rain and dispersal were efficient enough to reach every point and not to limit the recruitment.

The interaction of the understorey vegetation with the presence of juveniles was evidenced for the study species, but for *F. sylvatica* sites where the understorey vegetation was rather suppressed. Many works have previously investigated plant–plant interactions along gradients of environmental severity (Callaway and Walker, 1997), with compelling evidence about the nurse effect exerted by shrubs on recruits in Mediterranean and at high elevation areas (Castro et al., 2004; Batllori and Gutierrez, 2008; Batllori et al., 2009; Benavides et al., 2013; Grau et al., 2013; Caldeira et al., 2014; Tíscar and Linares, 2014). Accordingly, we detected this positive effect over the occurrence and abundance of juveniles of both pine species under moderate covers of shrubs (under 50% of cover), which concurs with the results from Batllori et al. (2009), who reported a shift from facilitation to competition as shrub cover increased. Moreover, we found that this positive effect faded out at extreme temperatures (high temperatures for *P. nigra* and low and high temperatures for *P. uncinata*), suggesting that facilitation disappears when the external conditions become more stressful (Maestre et al., 2005; Tíscar and Linares, 2014). On the other hand, we did not consider in this study the species identity effect of the shrubs, factor that may be crucial in fading or neglecting this

nursing effect due to, for instance, allelopathic effects, architecture or herbivory appeal (Gómez-Aparicio et al., 2004; Baraza et al., 2006).

Herbs compete with seedlings for resources (Davis et al., 1999), and in Mediterranean ecosystems this competition is mainly for soil water (Rey Benayas et al., 2005; Cuesta et al., 2010; Caldeira et al., 2014). This is in accordance with the negative effect that herb cover had on the abundance of our two Mediterranean species, *Q. ilex* and *P. nigra*, being especially relevant for the latter at high temperatures, where the heat-stress and drought conditions were greater. These indirect effects over recruitment have already being highlighted in previous studies with *Q. ilex* and other Mediterranean species, showing the complexity of plant–plant interactions, that not only fluctuate among years with the annual variation in climatic conditions (Holmgren et al., 2012), but also may interact with other biotic conditions not considered in our study, such as the canopy, the size or the age of the recruits (Cuesta et al., 2010; Benavides et al., 2013; Caldeira et al., 2014).

5. Conclusions

In this study we have surveyed the natural recruitment patterns of four tree species along entire elevational ranges to disentangle the different factors that, acting hierarchically, determine the regeneration patterns, in terms of occurrence, abundance and growth of recruits. The regeneration is a rather stochastic process, difficult to model due to the high variability in space (from regional to microhabitat scales), time (among years and within a year) and nature (abiotic and biotic including anthropogenic) of the factors involved. In this line, the performance of our models was modest, especially for *F. sylvatica*, whose sample size was limited, but agreed with the already reported difficulty for modelling this process in nature (Klopcic et al., 2012).

We acknowledge that an important driver for mid- and long-term patterns has been left out in this study, changes in the land use and management (*e.g.* coppicing abandonment, free-range livestock disappearance, specific species-oriented management, etc.). Notwithstanding, we elicited some important results that can shed some light on the complex net of nested factors that influence the natural regeneration of the study species. The four species have shown high responsiveness to climatic variables (regional scale), especially in terms of abundance and growth, with species influenced either by precipitation (*P. nigra* and *F. sylvatica*) or both precipitation and temperature (*Q. ilex* and *P. uncinata*). Moreover, we detected within species an ontogenetic differential sensitivity to climate (seedlings being more sensitive that saplings), and with different environmental factors influencing the growth at different age classes. Light availability, as a direct consequence of the stand structure (local scale), exerted an overall positive effect on juvenile growth regardless of the age. Finally, variables at micro-habitat scale played also a relevant role for the distribution models, supporting the competitive ability of herbs and the facilitative role (with restriction) of shrubs reported in previous studies; and at the same time, they modulated the effect of climate, exacerbating its negative effect on recruitment in heat-stressful places through competition or mitigating it through the nurse effect. These results and together with the disturbing climatic projections (Giorgi and Lionello, 2008; Nogués-Bravo et al., 2008), seem a powerful argument to encourage forthcoming managements to pay more attention to these local variables in Mediterranean areas considering the idiosyncrasy of each species, population and site. In particular, our results stand for boosting regeneration by promoting some cover of shrubs that facilitates recruitment success (especially for pines), removing the herb layer in more arid places or creating gaps to favor the juveniles' growth (*e.g.* adjusting the frequency and intensity of intermediate cuttings). Nevertheless, further studies are required to better understand how the local heterogeneity can contribute to mitigate the effects of the ongoing global warming along environmental gradients, and to avoid the natural regeneration failure.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2015.10.043.

References

Affleck, D.L.R., 2006. Poisson mixture models for regression analysis of stand level mortality. Can. J. For. Res. 36, 2994–3006.

Ameztegui, A., Coll, L., 2011. Tree dynamics and coexistence in the montane-subalpine ecotone: the role of different light-induced strategies. J. Veg. Sci. 29, 1049–1061.

Ameztegui, A., Coll, L., 2013. Unraveling the role of light and biotic interactions on seedling performance of four Pyrenean species along environmental gradients. For. Ecol. Manage. 303, 25–34.

Ameztegui, A., Coll, L., 2015. Herbivory and seedling establishment in Pyrenean forests: influence of micro- and meso-habitat factors on browsing pressure. For. Ecol. Manage. 342, 103–111.

Bakkenes, M., Alkemade, J.R.M., Ihle, F., Leemans, R., Latour, J.B., 2002. Assessing effects of forecasted climate change on the diversity and distribution of European higher plants for 2050. Glob. Change Biol. 8, 390–407.

Baraza, E., Zamora, R., Hódar, J.A., 2006. Conditional outcomes in plant-herbivore interactions: neighbours matters. Oikos 113, 148–156.

Barbeito, I., Dawes, M.A., Rixen, C., Senn, J., Bebi, P., 2012. Factors driving survival and growth at treeline: a 30-year experiment of 92000 trees. Ecology 93, 389–401.

Batllori, E., Camarero, J.J., Ninot, J.M., Gutiérrez, E., 2009. Seedling recruitment, survival and facilitation in alpine Pinus uncinata tree line ecotones. implications and potential responses to climate warming. Glob. Ecol. Biogeogr. 18, 460–472.

Batllori, E., Gutierrez, E., 2008. Regional tree line dynamics in response to global change in the Pyrenees. J. Ecol. 96, 1275–1288.

Benavides, R., Escudero, A., Coll, L., Ferrandis, P., Gouriveau, F., Hódar, J.A., Ogaya, R., Rabasa, S.G., Granda, E., Santamaría, B.P., Martínez-Vilalta, J., Zamora, R., Espelta, J.M., Peñuelas, J., Valladares, F., 2015. Survival vs. growth trade-off in early recruitment challenges global warming impacts on Mediterranean mountain trees. Perspect. Plant Ecol., Evol. Syst. http://dx.doi.org/10.1016/j.ppees.2015.06.004.

Benavides, R., Montes, F., Rubio, A., Osoro, K., 2007. Geostatistical modelling of air temperature in mountainous region of northern Spain. Agric. For. Meteorol. 146, 173–188.

Benavides, R., Rabasa, S.G., Granda, E., Escudero, A., Hódar, J.A., Martínez-Vilalta, J., Rincón, A., Zamora, R., Valladares, F., 2013. Direct and indirect effects of climate on demography and early growth of Pinus sylvestris at the rear edge: changing roles of biotic and abiotic factors. PLoS One 8, e59824.

Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H., White, J.S.S., 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends Ecol. Evol. 24, 127–135.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: A Practical Information-theoretic Approach. Springer, New York, USA, 488 p.

Caldeira, M.C., Ibañez, I., Nogueira, C., Bugalho, M.N., Lecomte, X., Moreira, A., Pereira, J.S., 2014. Direct and indirect effects of tree canopy facilitation in the recruitment of Mediterranean oaks. J. Appl. Ecol. 51, 349–358.

Callaway, R.M., Walker, L.R., 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. Ecology 78, 1958–1965.

Carnicer, J., Coll, M., Pons, X., Ninyerola, M., Vayreda, J., Peñuelas, J., 2014. Large-scale recruitment limitation in Mediterranean pines, the role of Quercus ilex and

forest successional advance as key regional drivers. Glob. Ecol. Biogeogr. 23, 371–384.

Castro, J., Zamora, R., Hódar, J.A., Gómez, J.M., 2004. Seedling establishment of a boreal tree species (*Pinus sylvestris*) at its southernmost distribution limit: consequences of being in a marginal Mediterranean habitat. J. Ecol. 92, 266–277.

Castro, J., Zamora, R., Hódar, J.A., Gómez, J.M., 2005. Alleviation of summer drought boosts establishment success of *Pinus sylvestris* in a Mediterranean mountain: an experimental approach. Plant Ecol. 181, 191–202.

Coll, M., Peñuelas, J.M., Ninyerola, M., Pons, X., Carnicer, J., 2013. Multivariate effects driving forest demographic responses in the Iberian Peninsula. For. Ecol. Manage. 303, 195–209.

Collins, R.J., Carson, W.P., 2004. The effects of environment and life stage on *Quercus* abundance in the eastern deciduous forest, USA: are sapling densities most responsive to environmental gradients? For. Ecol. Manage. 201, 241–258.

Cuesta, B., Villar-Salvador, P., Puértolas, J., Jacobs, D.F., Rey Benayas, J.M., 2010. Why do large, nitrogen rich seedlings better resist stressful transplanting conditions? A physiological analysis in two functionally contrasting Mediterranean forest species. For. Ecol. Manage. 260, 71–78.

Davis, M.A., Wrage, K.J., Reich, P.B., Tjoelker, M.G., Schaeffer, T., Muermann, C., 1999. Survival, growth, and photosynthesis of tree seedlings competing with herbaceous vegetation along a water-light-nitrogen gradient. Plant Ecol. 145, 341–350.

Doak, D.F., Morris, W.F., 2010. Demographic compensation and tipping points in climate-induced range shifts. Nature 467, 959–962.

Dobrowski, S.Z., 2011. A climatic basis for microrefugia: the influence of terrain on climate. Glob. Change Biol. 17, 1022–1035.

Espelta, J.M., Riba, M., Retana, J., 1995. Patterns of seedling recruitment in West Mediterranean coppiced holm oak (*Quercus ilex*) forests as influenced by canopy development. J. Veg. Sci. 6, 465–472.

Fortin, M., De Blois, J., 2007. Modeling tree recruitment with zero-inflated models: the example of hardwood stands in southern Quebec, Canada. For. Sci. 53, 529–539.

Galiano, L., Martínez-Vilalta, J., Lloret, F., 2010. Drought-induced multifactor decline of Scots pine in the Pyrenees and potential vegetation change by the expansion of co-occurring oak species. Ecosystems 13, 978–991.

Giorgi, F., Lionello, P., 2008. Climate change projections for the Mediterranean region. Glob. Planet. Change 63, 90–104.

Gómez-Aparicio, L., 2008. Spatial patterns of recruitment in Mediterranean plant species: linking the fate of seeds, seedlings and saplings in heterogeneous landscapes at different scales. J. Ecol. 96, 1128–1140.

Gómez-Aparicio, L., García-Valdés, R., Ruíz-Benito, P., Zavala, M.A., 2011. Disentangling the relative importance of climate, size and competition on tree growth in Iberian forests: implications for forest management under global change. Glob. Change Biol. 17, 2400–2414.

Gómez-Aparicio, L., Zamora, R., Gómez, J.M., Hódar, J.A., Castro, J., Baraza, E., 2004. Applying plant facilitation to forest restoration: a meta-analysis of the use of shrubs as nurse plants. Ecol. Appl. 14, 1128–1138.

Grau, O., Ninot, J.M., Cornelissen, J.H.C., Callaghan, T.V., 2013. Similar tree seedling responses to shrubs and to simulated environmental changes at Pyrenean and subarctic treelines. Plant Ecol. Divers. 6, 329–342.

Grubb, P.J., 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. Biol. Rev. 52, 107–145.

Gworek, J.R., Wall, S.B.V., Brussard, P.F., 2007. Changes in biotic interactions and climate determine recruitment of Jeffrey pine along an elevation gradient. For. Ecol. Manage. 239, 57–68.

Hall, D.B., 2000. Zero-inflated Poisson and binomial regression with random effects: a case study. Biometrics 56, 1030–1039.

Hampe, A., Petit, R.J., 2005. Conserving biodiversity under climate change: the rear edge matters. Ecol. Lett. 8, 461–467.

Harper, J., 1977. Population Biology of Plants. Academic Press, London, UK, p. 892.

He, F.L., Duncan, R.P., 2000. Density-dependent effects on tree survival in an old-growth Douglas fir forest. J. Ecol. 88, 676–688.

Herrero, A., 2012. *Capacidad de respuesta al estrés ambiental de poblaciones de Pinus sylvestris y Pinus nigra en el límite sur de distribución: una aproximación multidisciplinar.* PhD Thesis. University of Granada, Spain.

Holmgren, M., Gómez-Aparicio, L., Quero, J.L., Valladares, F., 2012. Non-linear effects of drought under shade: reconciling physiological and ecological models in plant communities. Oecologia 169, 293–305.

Jordano, P., Herrera, C.M., 1995. Shuffling the offspring – uncoupling and spatial discordance of multiple stages in vertebrate seed dispersal. Ecoscience 2, 230–237.

Jump, A.S., Hunt, J.M., Peñuelas, J., 2007. Climate relationships of growth and establishment across the altitudinal range of *Fagus sylvatica* in the Montseny Mountains, northeast Spain. Ecoscience 14, 507–518.

Klopcic, M., Poljanec, A., Boncina, A., 2012. Modelling natural recruitment of European beech (*Fagus sylvatica* L.). For. Ecol. Manage. 284, 142–151.

Körner, C., 2007. The use of 'altitude' in ecological research. Trends Ecol. Evol. 22, 569–574.

Kunstler, G., Thuiller, W., Curt, T., Bouchaud, M., Jouvie, R., Deruette, F., Lepart, J., 2007. *Fagus sylvatica* L. recruitment across a fragmented Mediterranean landscape, importance of long distance effective dispersal, abiotic conditions and biotic interactions. Divers. Distrib. 13, 799–807.

Lenoir, J., Gégout, J.C., Guisan, A., Vittoz, P., Wohlgemuth, T., Zimmermann, N.E., Dullinger, S., Pauli, H., Willner, W., Svenning, J.C., 2010. Going against the flow: potential mechanisms for unexpected downslope range shifts in a warming climate. Ecography 33, 295–303.

Lenoir, J., Gegout, J.C., Pierrat, J.C., Bontemps, J.D., Dhote, J.F., 2009. Differences between tree species seedling and adult altitudinal distribution in mountain forests during the recent warm period (1986–2006). Ecography 32, 765–777.

Linares, J.C., Tíscar, P.A., 2010. Climate change impacts and vulnerability of the southern populations of *Pinus nigra* subsp. *salzmannii*. Tree Physiol. 30, 795–806.

Lloret, F., Escudero, A., Iriondo, J.M., Martínez-Vilalta, J., Valladares, F., 2012. Extreme climatic events and vegetation: the role of stabilizing processes. Glob. Change Biol. 18, 797–805.

Lloret, F., Martínez-Vilalta, J., Serra-Díaz, J.M., Ninyerola, M., 2013. Relationship between projected changes in future climatic suitability and demographic and functional traits of forest tree species in Spain. Clim. Change 120, 449–462.

Lloret, F., Peñuelas, J., Prieto, P., Llorens, L., Estiarte, M., 2009. Plant community changes induced by experimental climate change: seedling and adult species composition. Perspect. Plant Ecol., Evol. Syst. 11, 53–63.

Maestre, F.T., Valladares, F., Reynolds, J.F., 2005. Is the change of plant–plant interactions with abiotic stress predictable? A meta-analysis of field results in arid environments. J. Ecol. 93, 748–757.

Matías, L., Gómez-Aparicio, L., Zamora, R., Castro, J., 2011. Effects of resource availability on plant recruitment at the community level in a Mediterranean mountain ecosystem. Perspect. Plant Ecol. Evol. Syst. 13, 277–285.

Matías, L., Zamora, R., Castro, J., 2012. Sporadic rainy events are more critical than increasing of drought intensity for woody species recruitment in a Mediterranean community. Oecologia 169, 833–844.

Moreno-Fernández, D., Cañellas, I., Barbeito, I., Sánchez-González, M., Ledo, A., 2015. Alternative approaches to assessing the natural regeneration of Scots pine in a Mediterranean forest. Ann. For. Sci. 72, 569–583.

Mutke, S., Gordo, J., Climent, J., Gil, L., 2003. Shoot growth and phenology modeling of grafted stone pine (*Pinus pinea* L.) in Inner Spain. Ann. For. Sci. 60, 527–537.

Ninyerola, M., Pons, X., Roure, J.M., 2005. Atlas Climático Digital de la Península Ibérica. Metodología y aplicaciones en bioclimatología y geobotánica. Universidad Autónoma de Barcelona, Bellaterra, Spain.

Nogués-Bravo, D., Araújo, M.B., Lasanta, T., López Moreno, J.I., 2008. Climate change in Mediterranean mountains during the 21st century. Ambio 37, 280–285.

Peñuelas, J., Boada, M., 2003. A global change-induced biome shift in the Montseny mountains (NE Spain). Glob. Change Biol. 9, 131–140.

Peñuelas, J., Ogaya, R., Boada, M., Jump, A.S., 2007. Migration, invasion and decline: changes in recruitment and forest structure in a warming-linked shift of European beech forest in Catalonia (NE Spain). Ecography 30, 829–837.

Pinheiro, J.C., Bates, D.M., 1995. Approximations to the log-likelihood function in the nonlinear mixed-effects model. J. Comput. Graph. Stat. 4, 12–35.

Quero, J.L., Herrero, A., Zamora, R., 2011. Linking stochasticity to determinism of woody plant recruitment in a mosaic landscape: a spatially explicit approach. Basic Appl. Ecol. 12, 161–171.

Rabasa, S.G., Granda, E., Benavides, R., Kunstler, G., Espelta, J.M., Ogaya, R., Peñuelas, J., Scherer-Lorenzen, M., Gil, W., Grodzki, W., Ambrozy, S., Bergh, J., Hódar, J.A., Zamora, R., Valladares, F., 2013. Disparity in elevational shifts of European trees in response to recent climate warming. Glob. Change Biol. 19, 2490–2499.

Rey Benayas, J.M., Navarro, J., Espigares, T., Nicolau, J.M., Zavala, M.A., 2005. Effects of artificial shading and weed mowing in reforestation of Mediterranean abandoned cropland with contrasting *Quercus* species. For. Ecol. Manage. 212, 302–314.

Ribbens, E., Silander, J.A., Pacala, S.W., 1994. Seedling recruitment in forests – calibrating models to predict patterns of tree seedling dispersion. Ecology 75, 1794–1806.

Silva, D.E., Rezende Mazzella, P., Legay, M., Corcket, E., Dupouey, J.L., 2012. Does natural regeneration determine the limit of European beech distribution under climatic stress? For. Ecol. Manage. 266, 263–272.

Thuiller, W., Lavorel, S., Araújo, M.B., Sykes, M.T., Prentice, I.C., 2005. Climate change threats to plant diversity in Europe. Proc. Natl. Acad. Sci. U.S.A. 102, 8245–8250.

Tiscar, P.A., Linares, J.C., 2011. *Pinus nigra* subsp. *salzmannii* forests from Southeast Spain: using structure and process information to guide management. In: Fisiras, C.T. (Ed.), Pine Forests: Types, Threats, and Management, Environmental Science, Engineering and Technology. Nova Science Publishers, pp. 279–314.

Tíscar, P.A., Linares, J.C., 2014. Large-scale regeneration patterns of *Pinus nigra* subsp. *salzmannii*: poor evidence of increasing facilitation across a drought gradient. Forests 5, 1–20.

Urbieta, I.R., García, L.V., Zavala, M.A., Marañón, T., 2011. Mediterranean pine and oak distribution in southern Spain: is there a mismatch between regeneration and adult distribution? J. Veg. Sci. 22, 18–31.

Vayreda, J., Gracia, M., Martínez-Vilalta, J., Retana, J., 2013. Patterns and drivers of regeneration of tree species in forests of peninsular Spain. J. Biogeogr. 40, 1252–1265.

Willms, J., Rood, S.B., Willms, W., Tyree, M., 1998. Branch growth of riparian cottonwoods: a hydrologically sensitive dendrochronological tool. Trees 12, 215–223.

Zamora, R., Gómez, J.M., Hódar, J.A., Castro, J., García, D., 2001. Effect of browsing by ungulates on sapling growth of Scots pine in a Mediterranean environment: consequences for forest regeneration. For. Ecol. Manage. 144, 33–42.

Zuur, A., Ieno, E.N., Walker, N., Saveliev, A.A., Smith, G.M., 2009. Mixed Effects Models and Extensions in Ecology with R. Springer, New York, USA, 574 p.

Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common statistical problems. Methods Ecol. Evol. 1, 3–14.